MICRO-ORGANISMS FROM THE LATE PRECAMBRIAN NARSSÂRSSUK FORMATION, NORTH-WESTERN GREENLAND

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ABSTRACT. Carbonaceous cherts of the late Proterozoic (*c.* 700 Ma) Narssârssuk Formation, north-western Greenland, contain about twenty microfossil entities distributed in four discrete microbial associations and one allochthonous association. The associations are the preserved remnants of cyanobacterial communities that inhabited different environments within the intertidal and supratidal zones of a hypersaline embayment bordering an arid sabkha-like coast. The palaeoecological distributions of Narssârssuk microbes are comparable to those of other fossil and modern microbial mats from similar environmental settings, suggesting that the Proterozoic evolution of the cyanobacteria has been characterized by physiological as well as morphological conservatism. Environmental explanations for observed differences in Proterozoic fossil assemblages provide the proper null hypothesis against which hypotheses of evolutionary change in stromatolitic cyanobacteria must be tested. Five new taxa are described: *Avictuspirulina minuta* gen. et sp. nov., *Coleogleba auctifica* gen. et sp. nov., *Gyalosphaera fluitans* gen. et sp. nov., *Eosynechococcus thuleënsis* sp. nov., and *Oscillatoriopsis variabilis* sp. nov.

FOSSIL assemblages of planktonic micro-organisms in Upper Proterozoic sedimentary rocks clearly indicate successive morphologic innovations and diversity trends with time (Vidal and Knoll, in press); however, the Precambrian record of benthonic stromatolitic microbiotas shows little evidence of temporal increase in morphologic diversity or complexity. Indeed, although the empirical success of stromatolite-based biostratigraphic correlations would argue for changes in the microbial benthos with time, most of the variation observable in Proterozoic stromatolitic microbiotas is attributable to palaeoecological factors. The reasons for this have to do with both preservational biases in the Precambrian record and the nature of evolution in prokaryotes.

The bulk of our detailed knowledge of Precambrian benthonic assemblages has been derived from the study of carbonaceous cherts in petrographic thin section. Silicification has the advantages that three-dimensional spatial relationships are retained and structures are often preserved at an extremely fine scale (0·5 μm) of resolution. It has the disadvantage that the variety of environments recorded is limited. Proterozoic cherts fall into two general categories: apparently primary cherts associated with iron formation, and silicified beds, lenses, and nodules found in laminated carbonates and stromatolites. Fossiliferous cherts from iron formations primarily contain benthic microfloras dominated by the problematic prokaryotes *Gunflintia* Barghoorn and *Huroniospora* Barghoorn or the trichosphaeric bacterium *Eoastrion* Barghoorn (Barghoorn and Tyler 1965; Cloud 1965; Walter, Goode and Hall 1976; Knoll and Simonson 1981; see also Oehler 1977, for a discussion of silicified microbes from an exhalative oceanic rift environment), although allochthonous elements do occur (e.g. *Leptoteichos*, Knoll, Barghoorn and Awramik 1978). These microbiotas differ considerably from those preserved in stromatolitic carbonates. Two general types of *in situ* stromatolite-building associations are known from the Proterozoic record: those dominated by colonies of the mucilage-producing coccoid cyanobacterium *Eoentophysalis* and those containing densely interwoven populations of filamentous blue-greens. *In situ* benthonic microbes not responsible for mat accretion may also be preserved, as in certain associations here described. Allochthonous elements, including transported fragments of pre-existing mats and plankton, are also found in mat assemblages (Knoll 1982*a*).

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In this paper, we describe a microbiota preserved in silicified carbonates of the late Proterozoic Narssârssuk Formation, north-western Greenland. All of the above-mentioned carbonate-facies fossil types, save ripped up mat clasts, are found within this sequence. Actually, four distinct microbial associations and one allochthonous assemblage representing a degree of habitat heterogeneity within the formation are preserved. These are comparable, in part, to both modern microbial communities in analogous depositional settings and to other Precambrian microfossil assemblages, thus, offering some insight into the distribution of cyanobacterial mat communities in time and space.

GEOLOGICAL SETTING AND AGE

The Thule Group is an Upper Proterozoic sedimentary sequence located in north-western Greenland between two structural highs, one south of Wolstenholme Fjord (76° 30′ N.) and the other in southern Prudhoe Land (approximately 78° N.; see text-fig. 1). The geology of the Thule region was outlined in 1959 by Kurtz and Wales, who divided the sequence into three formations: The Wolstenholme Quartzite (lowermost), the Danish Village Formation, and the Narssârssuk Formation. Davies, Krinsley and Nicol (1963) renamed the middle unit the Dundas Formation and, in addition, subdivided the Narssârssuk Formation into three members.

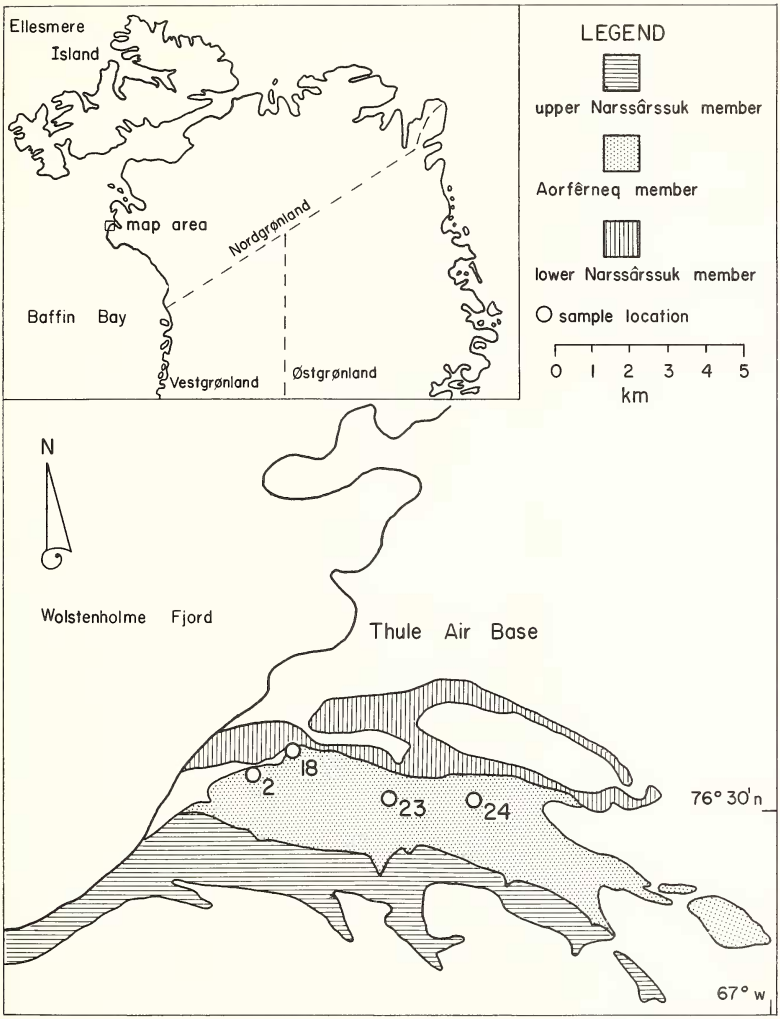
The Wolstenholme Quartzite is a 700 m unit consisting predominantly of white to grey quartz arenites, with subordinate intercalations of reddish sandstones near the base of the formation. Uppermost Wolstenholme beds grade into the dark shales and siltstones of the overlying Dundas Formation. The Dundas consists of approximately 730 m of organic-rich fine-grained detrital rocks with lighter (light-brown) units becoming more common in upper portions of the formation. Ripple marks, desiccation cracks, and load casts below thin sandstone intercalations indicate a near shore sedimentary environment, perhaps a lagoon or periodically flooded mud flat.

The youngest unit in the Thule Group, the Narssârssuk Formation, is characterized by a series of lithological cycles beginning with blocky limestones and grading upward through a succession of stromatolitic limestones and dolomites to thinly laminated dolomites capped by red siltstones. A limonitic erosional surface generally separates red beds from the overlying carbonates of the next cycle. The Lower and Upper Narssârssuk Members contain significant amounts of red siltstone; within the intervening Aorfêrneq Dolomite Member, such detrital beds are few and thin.

Multicycle sections of the Lower Narssârssuk Member record the repeated progradation of a sabkha-like plain across a protected hypersaline embayment which is similar in many respects to Mesozoic sabkha cycles of the Arab-Darb Formation of the Trucial Coast (Wood and Wolfe 1969). Lower Narssârssuk beds contain few sedimentary structures indicative of current movement. Microbially laminated carbonates are common, with low conical, apparently subtidal stromatolites (cf. *Conophyton* sp., see Hoffman 1976, for a paleoenvironmental analysis of this stromatolite type) in lower parts of the cycle giving way to flat, wavy cryptalgal laminites in overlying beds. Vuggy, gypsiferous units are associated with increasing clastic content in upper carbonates that grade into thinly bedded, organic rich shales and, ultimately, silty redbeds.

The Upper Narssârssuk Member is in many respects similar to the Lower, but contains a significantly greater percentage of detrital beds and also shows much more evidence of current activity. Cross-bedded calcareous sandstones often underlie the redbeds in the regressive cycle. Ripple marks are common, as are desiccation cracks in the red siltstones. Stromatolites in the Upper Narssârssuk Member differ from those of the Lower Narssârssuk, presumably in response to a stronger current regime. *Bicaulia*?-type columnar stromatolites were observed at one horizon, and oncolites at several others. Low relief domal stromatolites are also found in the Upper Narssârssuk.

Neither the Upper nor the Lower Narssârssuk Members contain more than rare, scattered patches of chert, and those that do occur contain no fossils. In contrast to this, the Aorfêrneq Dolomite Member contains several horizons of silicified microbial mats, some of which are abundantly fossiliferous. As discussed in more detail below, all cherts appear to be of early diagenetic origin, replacing pre-existing carbonates and permineralizing microbial peats. Although the



TEXT-FIG. 1. Locality map of the Narssârssuk Formation.

Aorfêrneq Member is predominantly dolomitic, thin red siltstone horizons confirm that this member, like the others, comprises a series of progradational cycles. The Aorfêrneq Dolomite differs from the other members in that broad carbonate tidal flats persisted for relatively long periods of time during its deposition. '*Cryptozoon*' type, laterally linked, hemispherical stromatolites are found in subtidal units while oölites attest to shoaling coastal environments. Wavy-laminated, low relief stromatolites are common, and in at least one locality, centimetre-scale mammilate stromatolites occur. Gypsum is common, both as growths disrupting pre-existing microbial laminae and as secondarily developed features in fractures. Although gypsum is a characteristic feature of the Aorfêrneq Dolomite, bedded gypsum horizons characteristic of some evaporitic environments are not found in this member.

The fossiliferous units of the Narssârssuk Formation, then, vary from subtidal to supratidal along the border of a protected embayment in an arid to semi-arid environment. A reasonable modern analogue is the west coast of the Arabian (Persian) Gulf in Abu Dhabi and elsewhere (Purser 1973; Kendall 1979). This provides an appropriate palaeoenvironmental context for the interpretation of Narssârssuk microbial associations.

In Prudhoe Land and the Wolstenholme Fjord region, sedimentary rocks of the Thule Group are cut by doleritic dykes and sills, several of which have been dated by K–Ar whole rock analyses (Dawes, Rex and Jepsen 1976). NW–SE trending dykes cutting the Dundas Formation yield a radiometric age of 676 ± 25 Ma. Similarly trending dykes cut the Narssârssuk Formation south of Wolstenholme Fjord, suggesting that the entire Thule Group is older than the date quoted. Palynomorphs recovered from the Dundas Formation indicate a late Riphean age (Vidal and Dawes 1980), and a single 'peteinosphaerid' (vandalosphaerid *sensu* Vidal 1981) acritarch found in lower Narssârssuk beds suggests an early Vendian age for this formation. Available evidence thus suggests that the Narssârssuk microbes lived during the early Vendian, approximately 700 Ma ago.

MICROFOSSIL ASSOCIATIONS

All samples discussed in this report were collected from the Aorfêrneq Member of the Narssârssuk Formation. Each locality received a locality number which is prefixed by 'KS 78-'. Four of our microfossil associations were restricted to unique localities, the *Gyalosphaera* association, however, was distributed among three separate localities, KS 78-2, KS 78-12, and KS 78-21. In addition, two of the associations, the *Eosynechococcus* and *Eomycetopsis*/*Siphonophycus* associations, occur together at only one locality, KS 78-23. These associations are referred to as '23U' and '23L', since they are derived from the upper and lower portions of the sample respectively. Additional letters suffixed to locality numbers refer to individual thin sections.

The Eosynechococcus *association* KS 78-23 [23U]

Locality KS 78-23, represented by a single chert sample from the middle portion of the Aorfêrneq Member, contains two quite distinct biological assemblages. The lower zone (Pl. 1, fig. 10, 23L) is dominated by vertically oriented filaments in a vuggy carbonate matrix and is capped by a zone of uniform carbonate grains which contains organic laminae but not fossils. The upper zone (Pl. 1, fig. 10, 23U), is a somewhat contorted, laminated siliceous layer containing a distinctive community dominated by a new species of *Eosynechococcus* Hofmann (1976). The basal portion of the upper zone is well preserved; however, subsequent layers are carbonate-rich and preservation is correspondingly variable. There is good evidence in this sample that silica emplacement occurred early during diagenesis, preserving the organisms in their growth positions.

The *Eosynechococcus* zone consists of about seven layers that range in thickness from 0·2 to 2·0 mm, each layer being defined by a kerogenous band at its base (Pl. 6, fig. 5). The layers are composed of equigranular carbonate and microcrystalline quartz (chert) in varying proportions. Carbonate crystals show dissolution surfaces, and void spaces within the carbonate layers are filled with fibrous quartz. The basal layer of the *Eosynechococcus* zone (Pl. 1, fig. 10) is composed entirely

of microcrystalline quartz which has faithfully preserved organic structural detail at the cellular level. Fossil micro-organisms are embedded in a homogeneous, amorphous, light-brown organic matrix that does not reflect quartz grain boundaries.

Two discrete microfossil populations dominate this assemblage, a rod-shaped cyanobacterium, *Eosynechococcus thuleënsis* sp. nov. and a problematic globular spheroid informally designated 'spheroid type A'. The filamentous cyanobacteria *Tenuofilum septatum* Schopf and *Oscillatoriopsis variabilis* sp. nov. also occur, but they are not abundant ($< 1\%$ of the total assemblage). Approximately 1% of the assemblage consists of large spherical organisms which probably represent an allochthonous element. The relative and absolute frequencies of microfossils within the basal layer of zone 23U are as follows ($N = 387$):

	Relative frequency	Abundance
Eosynechococcus thuleënsis	0·64	$1{\cdot}6 \times 10^4/cm^3$
Spheroid type A	0·35	$9{\cdot}0 \times 10^3/cm^3$
Planktonic spheroids	0·01	$200/cm^3$
Filaments	0·01	—

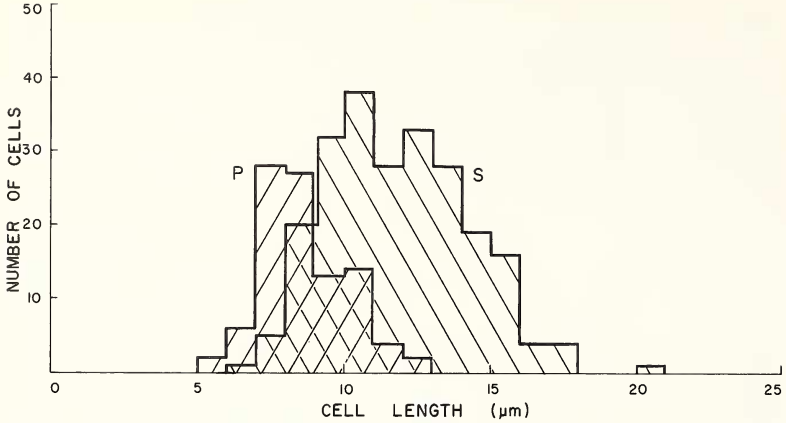
The total concentration of recognizable organisms within this zone is $2{\cdot}6 \times 10^4/cm^3$.

Cells of *Eosynechococcus thuleënsis* are usually preserved as straight or slightly curved rods with homogeneous contents that are similar in density to the surrounding organic matrix (Pl. 1, fig. 2). Some specimens exhibit dark, internal granules that are distributed along the long axis of the fossils rather than being condensed into discrete 'spots' as is common with certain Precambrian spheroids. The unilaminar walls of *E. thuleënsis* are uniform and smooth, suggesting that silicification has faithfully preserved the primary morphological features of the organism. Because the cells are never enclosed by concentric or co-parallel laminations that could be interpreted as sheaths, it is inferred that the living organisms did not have well-defined extracellular envelopes. Many *E. thuleënsis* cells are coated with exterior blebs of dense or vesicular organic matter (Pl. 1, figs. 4–6). These structures are probably artefacts of degradation. A degradational sequence runs from cells with a small number of attached blebs (Pl. 1, fig. 5) to clusters of small vesicles and blebs which correspond roughly to the original, elongate cell shape (Pl. 1, fig. 6). Similar structures are found attached to the codominant spheroid type A.

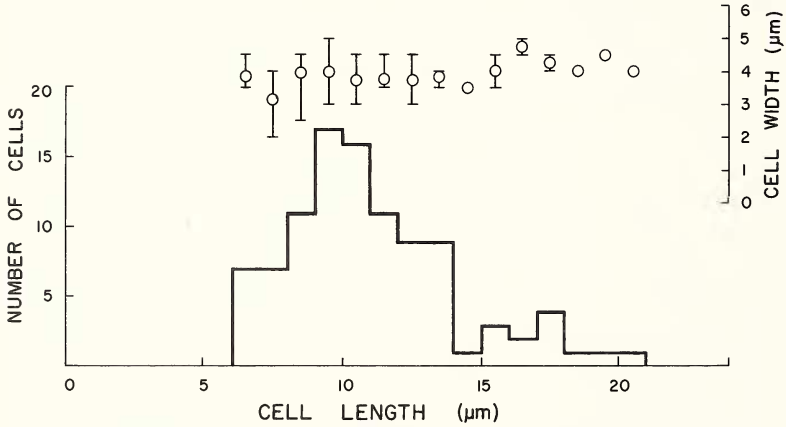
Many of the cells of *E. thuleënsis* are preserved as end-to-end pairs (Pl. 1, fig. 2) and it is this feature that permits elucidation of some growth characteristic of the original organism. Paired cells constitute 30% of the *E. thuleënsis* population (N = 759 from three thin sections). The mean length of paired cells is significantly less than that for solitary cells from the same population (text-fig. 2). In addition, the individual cells of a paired set are always approximately the same length. A sample population of forty-three paired sets of cells contained thirty-seven pairs (86%) whose lengths differed by 0·1 μm or less. The maximum difference between any two cells of a paired set was 0·4 μm. The total range in length of all cells of the population was 5 to 25 μm, therefore, paired sets of cells cannot be random associations of solitary cells. Rather, they must represent daughter cells which have remained attached end-to-end during diagenesis.

After dividing transversely, cells of *E. thuleënsis* grew by extension in length with no increase in girth (text-fig. 3). Therefore, cell width in *E. thuleënsis* is approximately constant and, consequently, cell length is proportional to volume.

The uniaxial growth of *E. thuleënsis* permits a more accurate assessment of cell size and increase than is possible with spherical cells. A detailed description of the size-frequency histogram for *E. thuleënsis* is helpful in confirming some of the assumptions about its life-history and ecology. For example, comparisons of paired sets of cells with solitary ones demonstrate that paired cells were derived by single transverse divisions of solitary cells (Strother 1980). The spatial distribution of the *E. thuleënsis* population permits the recognition of growth and development in this fossil form and indicates that the biotic association was of local benthonic derivation.



TEXT-FIG. 2. Length of paired (P) and solitary (S) cells in a population of *Eosynechococcus thuleënsis*.



TEXT-FIG. 3. Cell length vs. width of *Eosynechococcus thuleënsis*. Bar = range, circle = mean width.

Dominating the assemblage with *E. thuleënsis* is an enigmatic, irregularly shaped unicellular organism, spheroid type A (Pl. 1, fig. 3). Its cells are roughly spherical in outline, but cell shape is not uniform; often a spherical dark internal body is present. Cells do not exhibit any particular clustering habits that suggest growth patterns. The irregular envelope shape of spheroid type A suggests that it might be a degradational variant of *E. thuleënsis* which has lost its structural

integrity; however, calculated surface areas (for cells of minimum, mean, and maximum size) show no correlation between sample populations of the two organisms and size-frequency histograms for the two populations differ considerably. In addition, distinct cell pairs are absent from spheroid type A populations. The morphology of spheroid type A reveals little of its affinities to any known micro-organisms, extant or fossil.

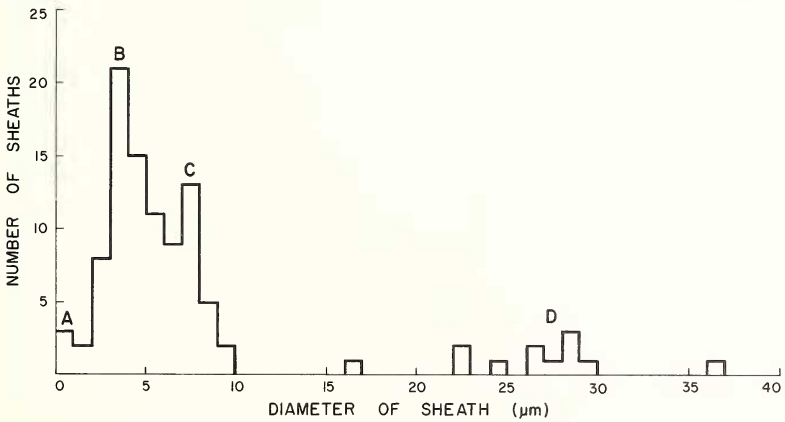
Ecologically, it appears that *E. thuleënsis*, spheroid type A, and the two co-occurring filaments lived as microbenthos in an area of periodic carbonate precipitation. There is little sedimentological or micropalaeontological evidence to suggest that zone 23U was stromatolitic in the sense of active trapping and binding or precipitation by microbes. More likely, this zone represents the passive trapping of surficial micro-organisms in abiogenic carbonates that were subsequently rapidly replaced by silica.

Eomycetopsis/Siphonophycus *association* KS 78-23 [23L]

Underlying the basal layer of the *Eosynechococcus* (23U) assemblage with profound micro-unconformity is a silicified filamentous assemblage named for its principal components. The texture of the filamentous zone is vuggy with densely clustered, vertically aligned, filaments (Pl. 1, fig. 9) interwoven between ovoid to rectangular voids that have been secondarily mineralized. Because they do not disrupt contiguous clusters of filaments, the voids are considered to be primary textural features (Pl. 6, fig. 5). Some filaments have served as nuclei for carbonate crystallization, retaining blocky crystals in their lumens despite general silicification (Pl. 1, fig. 7).

Most microfossils in the filamentous assemblage are empty cylindrical sheaths, although small pockets of spherical cells are sporadically distributed throughout the zone. Most spherical cells belong to *Sphaerophycus parvum* Schopf; however, occasional clusters of *Gloeodiniopsis* cf. *lamellosa* (Schopf) Knoll and Golubic are preserved (Pl. 5, fig. 7).

Filamentous sheaths can be divided into four taxa based on size distributions and sheath morphology. The smallest filaments are assigned to *Tenuofilum septatum* Schopf (text-fig. 4A). These range in diameter from 0·5 to 1·5 μm and consist of dark-brown, condensed strands of poorly preserved granular organic matter. *Eomycetopsis robusta* (Schopf) Knoll and Golubic is



TEXT-FIG. 4. Diameter of filamentous sheaths within KS78-23[L]. Letters mark modes of the four form taxa: A = *Tenuofilum*, B = *Eomycetopsis*, C = *Siphonophycus kestron*, D = *Siphonophycus* sp.

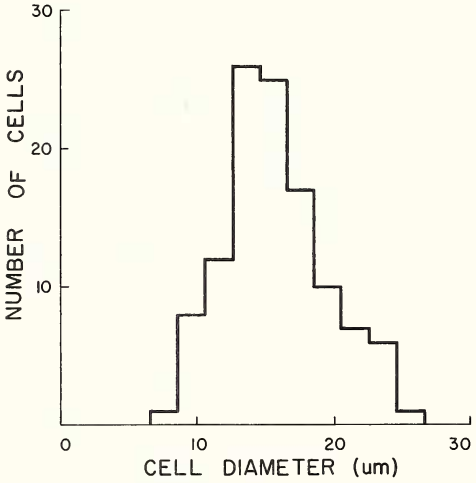
the most common sheath type (text-fig. 4B). Preservation is generally poor and sheath walls are usually composed of dark-brown, granular organic matter. The diameter ranges from over 3 μm to perhaps 6 μm, but at its maximum diameter, *E. robusta* cannot be distinguished with certainty from *Siphonophycus kestron* Schopf, the next larger sheath type in the distribution (text-fig. 4C). Poorly preserved specimens of *S. kestron* have granular walls, but well-preserved ones have discrete, 1 μm thick sheaths composed of light-brown, homogeneous organic matter. The largest sheaths in the assemblage (text-fig. 4D) are comparable to *Siphonophycus* sp. Oehler (1978) in size (20 to 40 μm), but they differ in occasionally containing the remains of internal trichomes (Pl. 1, fig. 8).

The retention of vertical filament orientations, the closely associated carbonate precipitation, and the position of vertical filament tufts as pillars between large voids suggest that this zone is best interpreted as a fossilized tufa deposit (Monty 1976; Hardie and Ginsburg 1977).

The Gyalosphaera *association* KS 78-2/12/21

These three localities from the middle of the Aorfêrneq Member of the Narssârssuk Formation contain microbial assemblages that are indistinguishable from each other and so are discussed as a single recurrent unit. Well-preserved microfossils are found in sinous 2 to 10 cm thick chert bands which are interbedded with fenestrate stromatolitic carbonate and gypsum (Pl. 6, figs. 1, 2). The carbonate portions of these samples are kerogen-rich, but unfossiliferous. Although some recrystallization of carbonate has occurred, certain features of primary mat texture are evident. The abundance of spherical colonies throughout the samples indicates minimal compaction during diagenesis for much of the chert. Euhedral carbonate rhombs with dissolution surfaces and some secondary fluorite crystals are scattered throughout the siliceous zone.

Two spheroidal organic structures dominate the biotic assemblage in these samples. The first is designated 'spheroid type B'. This organism is always faintly preserved because the density of organic matter within the organism is close to the matrix density. High contrast images (Pl. 2, figs. 1–3) reveal a spherical unicellular organism averaging 15·7 μm ($N = 113$) in diameter (text-fig. 5). Cell contents are homogeneous, though generally more dense centripetally. Spheroid type



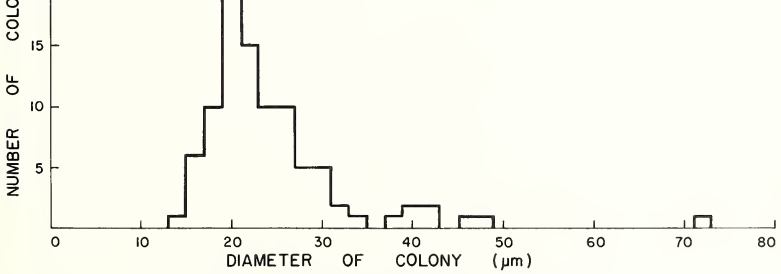
TEXT-FIG. 5. Diameter of a population of Spheroid type B.

B lacks any indication of lamination, either in the form of envelope or intracellular differentiation. Rare specimens of spheroid type B are lobed to elongate (Pl. 2, fig. 2). We have not observed examples with deep median furrows, but shallow furrows on elongate specimens imply a division mechanism. The size-frequency distribution for spheroid type B is leptokurtic and slightly positively skewed. Such a distribution is similar to populations of fossil algal unicells. Spheroid type B constitutes 79% of the organisms in the *Gyalosphaera* association.

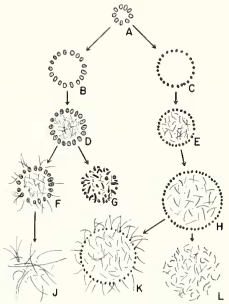
A second spherical structure, *Gyalosphaera*, constitutes 20% of the assemblage, with the remaining taxa comprising less than 1% of the total. *Gyalosphaera* is a spherical colony composed of numerous individual cells which lie at the surface of the sphere. The colony interior shows no evidence of cellular differentiation but is composed of condensed heterogeneous organic debris (Pl. 2, figs. 4–8). Individual cells, or spherules, appear as small (1 to 2 μm) vesicles, or they may be condensed to dark, oblate to polyhedral blebs (Pl. 2, figs. 6–8). Surficial views of large specimens reveal that the spherules are uniformly distributed (Pl. 2, fig. 5). Estimates of number of spherules per colony range from 200 to 4,500 cells. Individual estimates do not correspond to values of 2^n, therefore cell division within colonies was probably not rigidly co-ordinated, and the total number of spherules per colony was indeterminate. Clues to the reproduction of *Gyalosphaera* are lacking. *Gyalosphaera* colonies are never found associated with an encompassing envelope.

Gyalosphaera exhibits gradational variation in size and morphology. Increase in size is expected to reflect colony growth, consequently the histogram for *Gyalosphaera* (text-fig. 6) demonstrates the likelihood that both young and old members of populations have been preserved. Morphologic variation can be biological or diagenetic in origin. As illustrated in text-fig. 7, within *Gyalosphaera* populations, variation is expressed as a change in internal structure from uniform to heterogeneous (e.g. B to D), by the appearance of filamentous structures (F, J, K), in differences in spherule size (B line vs. C line), by spherule loss (J and L), and by coalification and degradation (G).

One specimen of *Gyalosphaera* cf. *fluitans* from slide KS 78-23/f has retained both the surficial spherule pattern and some of the interior structure. The spherules are grouped in sets of four pairs which are orthogonal. In median view (Pl. 2, fig. 11) some spherules can be seen to be attached to bifurcating stalks. This colony organization is similar to that found in the extant cyanobacterial genus, *Gomphosphaeria*, although the size of *Gyalosphaera* cf. *fluitans* is smaller than that of most *Gomphosphaeria* species. In general aspect, *Gyalosphaera* resembles the cyanobacterial genera



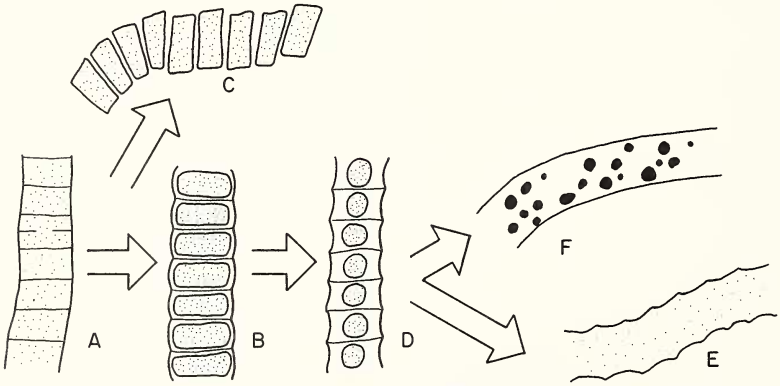
TEXT-FIG. 6. Colony diameter in *Gyalosphaera fluitans*.



TEXT-FIG. 7. Variation in colony form in *Gyalosphaera fluitans*. A–L, see text for explanation.

Gomphosphaeria and *Coelosphaerium* both of which consist of a surficial layer of cells defining a spherical colony. *Coelosphaerium* has an extracellular envelope of mucilage and colonies divide by fragmentation, neither of which has been observed in *Gyalosphaera* populations. In spite of these differences, a general morphological correspondence between *Gyalosphaera* and modern cyanobacteria of the *Gomphosphaeria*/*Coelosphaerium* type seems inescapable. This comparison, coupled with the sporadic distribution of colonies as seen in thin section, suggests that *Gyalosphaera* was a member of the plankton in the restricted waters of the Narssârssuk embayment.

A number of other, less abundant taxa are preserved within this assemblage. The most common filament is *Oscillatoriopsis variabilis* sp. nov. In this cyanobacterium, trichome width ranges from 14 to 16 μm, cell length is about 8 μm, and trichome length reaches 540 μm. Primarily on the basis of cell size, a number of morphological variations, mostly degradational, were recognized as belonging to the same organism (text-fig. 8). Preservation grades from extremely well-preserved trichomes with homogeneous cell contents (Pl. 3, fig. 3; text-fig. 8A) to well-preserved trichomes with condensed contents (Pl. 3, figs. 5, 6, 11; text-fig. 8B, D) to empty trichomes or sheaths with



TEXT-FIG. 8. Degradational forms in *Oscillatoriopsis variabilis*. A–F, see text for explanation.

granular contents (Pl. 3, fig. 7; text-fig. 8E, F). In some specimens, the cell walls have decomposed leaving behind detached cells (Pl. 3, fig. 4; text-fig. 8C). The spool-shaped cells illustrated in Plate 3, fig. 6 and text-fig. 8 correspond to forms from the Bitter Springs and Belcher Islands biotas given the generic name *Halythrix* Schopf (Schopf 1968; Hofmann 1976). Much of this morphological variation is explained by either cell wall collapse (cytorrhysis) or protoplast shrinkage (plasmolysis) due to osmotic change during the early stages of degradation and silicification. *O. variabilis* is sporadically distributed in the sample suites from localities KS 78-2, 12, and 21, and individuals do not show preferential orientation relative to bedding. These facts, as well as the absence of evidence for extracellular sheath or mucilage production, suggest that *O. variabilis* cannot be considered as a major builder of the mats in which it is found.

Similarly, other filaments and unicells found in this assemblage are sporadically distributed; the actual organism or organisms responsible for mat accretion in this environment remain unknown. Post-mortem degradation must have proceeded quite effectively, leaving the preserved biota as scattered remnants of the original community. Thus, the palaeoecological interpretations that can be drawn for other microfossil associations in this formation and others (e.g. Knoll 1982*a*, 1982*b*) based on the spatial distribution of populations are difficult to apply in this case. Mineralogical evidence points toward a supratidal depositional environment; biotic evidence indicates an immediate environment of deposition which was plankton supporting. It is possible that *Gyalosphaera* association was a puddle-dwelling community within a supratidal zone.

Two species of *Eosynechococcus* occur as rare components of the *Gyalosphaera* assemblage. The more common of these is *E. thuleënsis*, found most often in carbonate-rich portions of the chert. Nowhere in this assemblage, however, is *E. thuleënsis* so extensively developed as it is in the *Eosynechococcus* association. The second species of *Eosynechococcus* found in association with *Gyalosphaera* is *E. amadeus* Knoll and Golubic (1979) (Pl. 3, figs. 8, 10), originally described from the Bitter Springs Formation. The similarity in size, shape, and clustering habit between the Bitter Springs and Narssârssuk *E. amadeus* populations (Pl. 3, fig. 8) are among the most striking yet observed in Precambrian palaeontology. Other chroococcalean unicells that occur in the *Gyalosphaera* association include *Sphaerophycus parvum* Schopf; small (2 by 3 μm) paired, ensheathed coccoid cells; and large (15 to 16 μm in diameter) poorly preserved dyads and tetrads (Pl. 4, fig. 1).

Two other filamentous organisms also occur as rare elements in the *Gyalosphaera* association. The first is an *Oscillatoriopsis* sp. which has a trichome width of 8 μm and a cell length of 10 to 12 μm (Pl. 3, fig. 7). Too few specimens have been found to characterize this fossil at the specific level; however, the preservation of internal structure is similar to that in *O. variabilis*. The second is a small spiral trichome found in association with large *Gyalosphaera* colonies or as isolated individuals scattered throughout the fossiliferous horizons. The trichome is 0·8 μm wide, non-septate, and coiled into a loose spiral 5 to 9 μm in diameter. This form is new to Precambrian paleobotany and is placed in the new genus, *Avictuspirulina*, based on morphological congruence with the extant genus, *Spirulina* Turpin em. Gardner (Pl. 3, fig. 9).

The Eoentophysalis *association* KS 78-18

Distinctive, mamillate stromatolites, in part silicified, occur in the lowermost beds of the Aorfêrneq Dolomite Member exposed at an abandoned NIKE site near Thule Air Force Base. The stromatolites (Pl. 6, figs. 3, 4) are centimetre-scale, laterally linked hemispheroids (LLH-type of Logan, Rezak and Ginsburg 1964) similar in morphology to mats accreting in modern intertidal zones bordering protected embayments in Abu Dhabi and the Bahamas (Golubic and Hofmann 1976). The modern stromatolites are built by colonies of the gregarious, mucilage-producing coccoid cyanobacterium *Entophysalis*, and it is clear from *in situ* microfossils preserved in silicified portions of the Narssârssuk structures that these were built by morphologically comparable organisms assignable to the genus *Eoentophysalis* Hofmann (1976).

Eoentophysalis is characterized by small (< 10 μm) cells that divide in three planes to form dense aggregates of monads, dyads, and tetrads embedded in a common mucilage or encompassed by common extracellular envelopes (Pl. 4, fig. 3). Indeed, the extracellular envelopes, which often

retain a record of cell-division patterns, are more resistant to post-mortem degradation than are the cells *per se* and may constitute the bulk of the preserved microfossil population (Golubic and Hofmann 1976; Knoll and Golubic 1979). As in modern *Entophysalis* colonies, *Eoentophysalis* aggregates in the Narssârssuk Formation vary in structure from palisade-like arrays (Pl. 4, fig. 7), to globular clusters (Pl. 4, figs. 4–6), to loosely aggregated, irregular groups of cells (Pl. 4, fig. 8). The latter type is the most common cluster arrangement in the fossil populations; individuals (cells or unit envelopes) per cluster range from ten or a few tens to several hundred. Some aggregates contain well-preserved individuals on the cluster periphery with degraded envelopes or amorphous organic matter in the interior. Lack of mineralogical difference between the exterior portions of clusters suggests that this feature is degradational rather than mineralogically produced. Thus, cells grew centrifugally, leaving behind a degraded mucilaginous centre, a pattern common to both modern and fossil entophysalid cyanobacteria (Golubic and Hofmann 1976).

Narssârssuk *Eoentophysalis* individuals are spherical to ellipsoidal and range from 2·5 to 9·0 μm in maximum diameter. Thus, at the lower end of the size range, some populations closely resemble populations of *S. parvum* Schopf (see Knoll and Golubic 1979). Certainly, the types of these two taxa represent different cyanobacteria, but populations of small individuals within *Eoentophysalis* mats that are assigned to *S. parvum* may be biological and/or degradational variants of *Eoentophysalis*. This appears to be the case, in part, in the Narssârssuk Formation; however, we do not wish to extend this interpretation to other formations that contain *Eoentophysalis* and *S. parvum* in intimate association, not having seen the necessary materials in thin section.

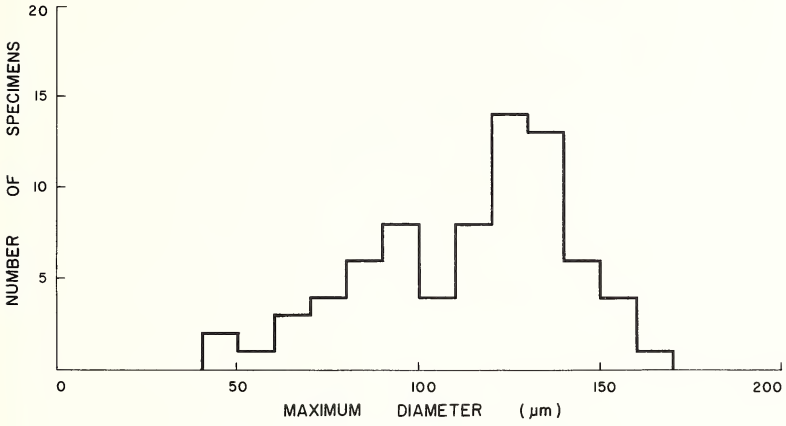
Cell contents of Narssârssuk *Eoentophysalis* vary from uniformly dense interiors (Pl. 4, fig. 7) with minimal sheath retention to clear or very lightly stained interiors (Pl. 4, figs. 3, 8). Most of the various degradational forms of individual cells correspond to the '*capsulata*' form of *E. belcherensis* Hofmann (1976). Cell contents are not condensed to dark 'spots', but, rather, degradation has caused either loss of contents with retention of the exterior envelope or uniform condensation of the entire cell. *Eoentophysalis* from the KS 78-18 site does not form the differentially pigmented laminae illustrated in Pl. 4 of Hofmann (1976). The other salient features of *E. belcherensis* are present, however, thus the designation *Eoentophysalis* cf. *belcherensis* is appropriate.

Scattered throughout the preserved entophysalidaceae populations is an organism that is most likely an allochthonous element of the assemblage. *Coleogleba auctifica* gen. nov., sp. nov. is a large, spherical to globose colonial cyanobacterium enclosed within an extensive and well-defined mucilaginous envelope. Colony diameters range from 40 to 180 μm (text-fig. 9). Individual cells (spherules) within colonies are quite small usually 1 to 2 μm, and may be preserved as vesicles (Pl. 5, fig. 1) or, more commonly, as spherical granules of condensed organic matter (Pl. 5, figs. 2, 3). Individuals are distributed uniformly throughout the colony in an amorphous organic matrix. Surrounding sheath material is often laminated in larger specimens (Pl. 5, fig. 3), although smaller colonies may lack extensive extracellular mucilage (Pl. 5, fig. 1). The ensheathing material ranges from amorphous, dark, laminated envelopes (Pl. 5, fig. 3) to light coloured amorphous organic matter containing embedded spherules (Pl. 5, fig. 2).

A population of seventy-four *C. auctifica* colonies distributed along a single bedding plane was measured for maximum diameter and the corresponding histogram plotted in text-fig. 9. The distribution is left-skewed and unimodal with a mean of 114 μm. The shape of the histogram suggests colony replication characterized by peripheral growth of daughter colonies that remain attached to the parent colony. In such a situation, mature colonies do not significantly reduce their diameter during division, and a skewed size distribution results.

In the salient aspects of its colony morphology and divisional pattern, *Coleogleba* closely resembles species of the extant cyanobacterial genus *Microcystis* Kützing, although *Microcystis* colonies do not always retain the tight spheroidal organization exhibited by the fossils. Modern *Microcystis* populations most often occur as plankton in freshwater lakes, but Geitler (1932) does discuss species living as microbenthos in sandy intertidal zones (*M. reinboldi*), as plankton in littoral salt-water puddles (*M. litoralis*), and as plankton in standing water bodies of varying salinities (several species). The distribution of *Coleogleba* within the *Eoentophysalis* stromatolites suggests

that it, too, lived as plankton within the Narssârssuk embayment or in local evanescent ponds. *Coleogleba* colonies are, in so far as preservation allows us to comment, restricted to the *Eoentophysalis* association. The ability of entophysalid buildups to pond water in coastal environments has been documented for the Recent (this occurs at Hamelin Pool, Shark Bay, Western Australia) and suggested for other fossiliferous Precambrian formations (Knoll and Golubic 1979); it may be that *Coleogleba* populations thrived in such short-lived, localized habitats within the Narssârssuk intertidal zone.



TEXT-FIG. 9. Colony diameter of *Coleogleba auctifica*.

Poorly preserved filaments are found scattered throughout the silicified *Eoentophysalis* horizons. Almost all are sheaths, of which *Eomycetopsis* is the most common type. Although filaments intertwine, they do not show the preferred orientation that might be expected if they represented *in situ* mat builders. Sheaths of *Siphonophycus*, occasionally containing condensed trichomes, are also found in organic-rich portions of the chert. Only short lengths of these thicker tubes are preserved and, again, no preferred orientation is observed.

Various coccoid cells are common in this association. Several clusters of *Gloeodiniopsis* cf. *lamellosa* with multilaminate, thick-walled sheaths and diameters approaching 20 μm are found (Pl. 5, fig. 6), and one cluster of coccoid cells (Pl. 5, fig. 5) is referable to the genus *Tetraphycus* Oehler (1978). The latter population contains planar tetrads of cells approximately 5 μm in diameter. These fossils differ from other species of *Tetraphycus* by the differentiation of their interior cross walls and exterior envelope. Cell (sheath?) cross walls are smooth, whereas the external envelope is punctate. Such a pattern may be degradational, although too few specimens were located to assess this properly.

KS 78-24 *association*

In one horizon from the lower middle Aorfêrneq Dolomite Member, singularly spheroidal chert nodules have replaced anhydritic laminated dolomites. The microbiota of these nodules consists of sporadically and relatively poorly preserved unicells. Additionally, the nodules preserve 'chicken wire' structures of anhydrite crystals clusters replaced by silica (Pl. 6, fig. 6). Comparable sedimentary

features are known to occur in supratidal mats of the Arabian (Persian) Gulf (Wood and Wolfe 1969; Shearman 1978) and provide a unique clue to the palaeoenvironmental position of this sample. *S. parvum* and similarly simple spherical unicells are the most common microfossil types. They often exhibit various stages of degradation, including the condensation of internal granular, carbonized organic matter. A single occurrence of *Gloeodiniopsis* cf. *lamellosa* is similar to that illustrated in Pl. 5, fig. 6, and a second ensheathed chroococcalean cyanobacterium is shown in Pl. 4, fig. 2. Specimens of *Gyalosphaera* also occur, as do scattered carbonate infilled spheres that form clusters of poorly preserved dark, organic polygons (Pl. 5, fig. 4). Hofmann (1976, Pl. 3, figs. 8, 9) found similar fossils in the Kasegalik and McLeary Formations in Canada which he interpreted as acritarchs based on their polygonal shapes. Our specimens appear polygonal due to the inclusion of carbonate in the cell lumens, and it may be suggested that similar non-biological factors determined the morphology of the Belcher Island samples.

Summary of microfossil associations

The distributions and relative abundance estimates of the nineteen microfossil entities found in the Narssârssuk Formation are listed in Table 1. As discussed above, four well-defined microbial associations and one allochthonous assemblage are evident: a filamentous tufa association dominated by sheaths of filamentous cyanobacteria, a non-stromatolitic association dominated by *E. thuleënsis*, an entophysalidacean mat community with associated puddle-dwelling cyanobacteria,

	TAXON	KS78-23L	KS78-23U	KS78-2.12.21	KS78-18	KS78-24
SPHERES: COLONIES	Gyalosphaera fluitans n.g., n.sp.		R	A		
	Coleogleba auctifica n.g., n.sp.				C	R
	Tetraphycus sp.				R	
	Sphaerophycus parvum Schopf	R		R	A	R
	Eosynechococcus thuleënsis n.sp.		A	R		
	Eosynechococcus amadeus Knoll and Golubic			R		
	Eoentophysalis cf. belcherensis Hofmann				A	
	Myxococcoides sp.					R
	Gloeodiniopsis cf. lamellosa Schopf em. Knoll and Golubic	R				R
	Chroococcoid Type A			R		
	Chroococcoid Type B					R
	Spheroid Type A		A			
	Spheroid Type B		R	A		
FILAMENTS	Siphonophycus sp.	C				
	Siphonophycus kestron Schopf	C			R	
	Oscillotoriopsis variabilis n.sp.		+	C		
	Eomycetopsis robusta Schopf em. Knoll and Golubic	A			R	R
	Tenuofilum septatum Schopf	R	R			
	Avictuspirulina minuta n.g., n.sp			R		

TABLE 1. Distribution of Taxa with the Narssârssuk Formation. A = abundant (> 30%). C = common (30—1%), R = rare (< 1%), + = present in a single occurrence. Values are estimates and are, therefore, not quantitative.

an assemblage containing oscillatorian filaments and allochthonous colonial cyanobacteria, and an allochthonous assemblage containing mostly degraded spherical cells. No single association contains more than eight taxa, and in each case, one or two blue-greens completely dominate the preserved biota. The limited taxonomic overlap among associations is also clear from Table 1; no one species is listed as being abundant in more than a single association, although about half are found as rare elements of two or more associations.

The preserved biotas represent the degradation resistant residue of microbial communities distributed across the broad carbonate tidal flats of the Narssârssuk coast. Tufa-encased fossils would appear to have inhabited uppermost intertidal to supratidal habitats, as did the poorly preserved cells found with 'chicken wire' structures in locality KS 78-24. The mamillate entophysalidacean mats grew in the intertidal zone, while transient puddles of water dammed by the accreting stromatolites harboured a distinctive cyanobacterial population. The *Gyalosphaera* association (KS 78-2/12/21) is most difficult to place environmentally, but the combination of its sedimentological setting within the tidal flat zone, the presence of small nobs of disruptive calcium sulfate and fluorite within the microbially laminated dolomite, and the abundance of probable planktonic elements in the preserved assemblage suggests either a frequently flooded position within the intertidal zone or a ponded area higher in the tidal flat range.

DISCUSSION

As discussed above, sedimentological considerations suggest that the Narssârssuk Formation can, in general, be understood in terms of modern and coastal environments such as those bordering protected lagoons of the Arabian (Persian) Gulf. In Abu Dhabi, various microbial mat communities inhabit the broad tidal zone between the Khoral Bazam, a highly saline lagoon, and the prograding sabkha plain to the landward (Kendall and Skipwith 1968). Microbially laminated 'biscuits' built by the filamentous cyanobacterium *Phormidium hendersonii* Howe actually occur subtidally, and those give way sequentially to *Entophysalis*-built mamillate mats, flat mats dominated by *Microcoleus chthonoplastes* Thuret, and 'pinnacle' mats characterized by *Schizothrix splendida* Golubic as one ascends the intertidal zone (Golubic 1976). Park (1977) has discussed this microbial community zonation and suggested that the frequency and duration of wetting, itself a consequence of both tidal oscillations and evaporation rates, exerts a primary control on community distribution. In broad pattern, individual microbial associations occupy discrete zones running parallel to the shore-line, but this distribution can be complicated considerably by the presence of pools, channels, and puddles (Golubic 1976; Knoll and Golubic 1979; see also figure 7-D of Kendall and Skipwith 1968, p. 1050).

The *Eoentophysalis* association of the Narssârssuk Formation provides the best biological point of comparison between the modern and ancient environments. In terms of microbial morphologies, taxonomy, morphology of associated stromatolites, and position within the carbonate intertidal zone, the Greenland example appears to be strikingly similar to the modern. Other Narssârssuk assemblages can be related to the modern model only in more general terms, but it does appear that position along the subtidal to supratidal gradiant, complicated by ponding, controlled microbial distribution.

Entophysalid-dominated mat associations have been reported from a number of Proterozoic formations. The oldest such biota comes from approximately 2,000 m.y. old cherts of the Kasegalik and McLeary formations, Belcher Islands, Canada (Hofmann 1976) and, like the Narssârssuk occurrence, this Early Proterozoic association is strikingly similar to modern entophysalid mats in both biology and inferred environmental setting (Golubic and Hofmann 1976). Younger *Eoentophysalis*-dominated assemblages have been reported from the 1,500 m.y. Amelia Dolomite, Australia (Muir 1976), the slightly younger Balbirini Dolomite, also of Australia (Oehler 1978), the 1,400–1,500 m.y. old Gaoyuzhuang Formation, China (Zhang 1981), the 1,200 m.y. old Dismal Lakes Group, District of Mackenzie, NWT, Canada (Horodyski and Donaldson 1980), and the 750–790 m.y. Bitter Springs Formation, Australia (Knoll and Golubic 1979). Environmental settings

appear to be comparable in all cases, documenting the rather remarkable persistence of a unique community-type in a single environment throughout some 2,000 m.y. of earth history.

Filaments found within the Narssârssuk *Eomycetopsis*/*Siphonophycus* association are widely distributed in Proterozoic stromatolitic microbiotas, but the evolutionary or palaeoecological import of this observation is equivocal because the taxa in question—*Eomycetopsis*, *Syphonophycus*, and *Tenuofilum*—are form genera that in all likelihood were produced by several types of cyanobacteria. Certainly, the filaments of the Narssârssuk association are, to the best of our knowledge, unique among described Proterozoic microfossils in their preservation within a silicified supratidal tufa.

The dominant organisms in the other Narssârssuk associations, *Eosynechococcus thuleënsis*, *Gyalosphaera fluitans*, and *Oscillatoriopsis variabilis*, are sufficiently different from previously described microfossils to preclude meaningful palaeoecological comparisons.

CONCLUSIONS

The importance of environmental setting over age as a major theme in the interpretation of Proterozoic microbial mat assemblages was introduced by Hofmann (1976) and expanded by several other workers (e.g. Peat *et al.* 1978; Knoll and Golubic 1979; Knoll and Simonson 1981). Indeed, given available evidence, one is hard pressed to make a convincing case for either major morphological evolution in the cyanobacteria or increasing ecosystem complexity during the Proterozoic, except, perhaps, for the introduction of colonial planktonic cyanobacteria in the late Riphean. More taxa are known from younger Proterozoic sediments; however, it is clear that in terms of environments the younger Proterozoic is much better sampled than the earlier part of the eon (see Schopf 1977). In cases where the biology of a single environmental setting can be traced throughout most of the Proterozoic, e.g. *Eoentophysalis* mats, little evidence of progressive morphological or ecosystem change is evident.

Care must be exercised in extrapolating records of microbial species diversity based on cumulative tabulations of individual deposits. Evidence from the Aorfêrneq Dolomite Member of the Narssârssuk Formation, the Bitter Springs Formation (Knoll and Golubic 1979; Knoll 1981), and the Draken Conglomerate and Hunnberg Formation, Svalbard (Knoll 1982*a*, 1982*b*), demonstrates that cherty horizons from a single formation often preserve the records of biologically heterogeneous environments. Indeed, multiple assemblages can be found within a series of lamellae within a single hand specimen. Many, if not most, of these silica precipitating environments were hypersaline (e.g. Oehler, D. Z., Oehler, J.H. and Stewart 1979), and today similar habitats support microbial mat communities of low cyanobacterial diversity. The diversity of other bacteria, both photosynthetic and heterotrophic, within modern mats can be impressive (Krumbein *et al.* 1979; Margulis *et al.* 1980); however, the remains of these organisms evidently have a low preservation potential and have not been identified with certainty from ancient mat assemblages.

If one *is* to assess microbial evolution through the Proterozoic, one must base such evaluations on: (1) temporal changes in the diversity and/or community structure exhibited by microfossil associations from specific palaeoenvironments defined sedimentologically, or (2) the appearance of morphological innovations within biologically defined lineages. There is little evidence to support the first criterion; but, as mentioned above, new fossil forms do appear in younger rocks. Organizational complexity does show progressive increase throughout the Proterozoic record of planktonic cyanobacteria. For example, Schopf (1977) has noted a significant increase in the size of both spheroidal and filamentous microfossils approximately 1,400 m.y. BP which he attributes to the evolution of the enkaryotic cell. Evolution may account for some of the observed changes; however, environmental sampling cannot be ruled out as another causative factor. Pre-1400 m.y. microbial assemblages published to date include entophysalid-dominated, arid intertidal zone cyanobacterial biotas and Gunflint-type iron formation or deep water, exhalative ridge environment microfloras. The latter are unrepresented in younger deposits, although for the most part their microfossils have close morphological analogs in the modern prokaryotic biota; the former come

from an environment that in post-1,400 m.y. rocks still contains relatively small unicells and filaments.

The colonial chroococcalean cyanobacteria *Coleogleba* and *Gyalosphaera* in the Narssârssuk Formation do add a new element of morphological complexity to the Proterozoic fossil record. Hitherto, the most highly ordered pattern of cell division known in the Precambrian record of the Chroococcales was a report of *Eucapsis*(?) from the 1,600 m.y. old Paradise Creek Formation, Australia (Licari, Cloud and Smith 1969. *Eucapsis*(?) is characterized by regular binary division in three mutually perpendicular planes to form cubical colonies. *Gyalosphaera* represents a subsequent stage of chroococcalean evolution in which division in two planes is ordered on to the surface of a sphere. Still, the limited palaeontological sample of Precambrian ages and environments available to us suggests that it would be hazardous at this point to equate palaeontological first known appearance with evolutionary first appearance.

Certainly, prokaryotes have evolved over the past 2,000 m.y. years; in particular, the existence of specialized parasitic and symbiotic bacteria attest to this fact. Yet, palaeontological evidence indicates that the major features of the prokaryotic biota evolved rapidly and early, and were well-established some 2,000 m.y. ago. More specifically, it is quite possible that the morphological limits of variability of the cyanobacteria were realized during the Proterozoic and that subsequent natural selection has affected physiological processes rather than morphology. The recognition of such physiological evolution is potentially resolvable only through detailed comparative palaeoecological studies.

We do not wish to conclude by leaving the impression that the Proterozoic microfossil record does not and cannot exhibit critical evidence for cyanobacterial evolution. Rather we suggest that environmental explanations for observed differences in fossil assemblages provide the proper null hypotheses against which hypotheses of evolutionary change in mat-dwelling cyanobacteria must be tested.

SYSTEMATIC PALAEONTOLOGY

All specimens described herein are from black cherts from the Aorfêrneq Dolomite Member of the Narssârssuk Formation (Thule Basin) exposed south of Thule Air Base, north-west Greenland. Type material is housed in the Harvard Paleobotanical Collections (HPC) of the Paleobotanical Laboratories, Harvard University, Cambridge, Massachusetts, USA.

Kindom MONERA Haeckel, 1878
Phylum CYANOPHYTA Smith, 1938
Class COCOGONEAE Thuret, 1875
Family CHROOCOCCACEAE Nägeli, 1848
Genus GYALOSPHAERA gen. nov.

Type species. Gyalosphaera fluitans sp. nov.

Diagnosis. Fossilized spherical colony composed of peripheral, organically preserved unicells (spherules) in a common mucilage. Spherules may be spherical, ellipsoidal, vesicular (hollow), or condensed to granular bodies. Colony interior clear, filled with unorganized organic matter, or containing short rod-shaped structures. Spherule distribution uniform over colony surface. Outwardly projecting filaments, if present, attached singly throughout the colony or in tufts at colony surface. Extra-colonial sheath or membranes absent; larger colonies may produce some extra-colonial mucilage.

Etymology. From the Greek for 'hollow sphere'.

Gyalosphaera fluitans sp. nov.

Plate 2, figs. 4–11; Plate 3, figs. 1, 2

Diagnosis. As for genus but with spherules 0·5 to 3·0 μm in diameter; colonies from 12 to 100 μm

or greater in overall diameter; attached filaments, if present, 1 μm wide and 5 μm or greater in length.

Holotype. Figured in Pl. 2, figs. 6–8. Slide No. KS78-12h. England finder co-ordinates, H25/3. HPC No. 60465.

Etymology. From the Latin *fluitans* for 'floating', in reference to the planktonic life mode of this organism.

Discussion. *Gyalosphaera fluitans*, as described, may represent at least two biological species. The histogram in text-fig. 6 based on colony diameter reveals a slight break in the size distribution at 35 μm; however, this distinct-size partition is not matched by discontinuous variation in other morphological features—for example, spherule morphology. Thus, many of the larger forms (text-fig. 7H, K, L) are part of the size continuum that includes colonies less than 35 μm in diameter. The nature of associated filaments, which occur in less than 5% of the observed colonies, is obscure; attached filaments may represent biologically distinct degrading organisms. Certain very large spherical masses (Pl. 3, fig. 2; text-fig. 7L) appear to be related to *G. fluitans* based on the similarity of internal organic matter; however, similarities may result from degradational convergence of form and may not necessarily indicate close biological affinity. The geometric construction of *G. fluitans* is most similar to the extant genera *Gomphosphaeria* Kützing and *Coelosphaerium* Nägeli which are found in the plankton of freshwater habitats (although *Gomphosphaeria* has been reported from brackish and marine plankton (Humm and Wicks 1980)).

Gyalosphaera cf. *fluitans*

Plate 2, fig. 11

Discussion. One specimen of colonial form, similar in morphology to *G. fluitans*, was found in the *E. thuleënsis* mat in slide KS 78-23f. It is characterized by an evenly spaced paired arrangement of spherules which are attached to bifurcating stalks. This morphology is exactly analogous to that found in the extant cyanobacteria of the genus *Gomphosphaeria*.

Genus COLEOGLEBA gen. nov.

Type species. *Coleogleba auctifica* sp. nov.

Diagnosis. Fossilized multicellular colonies, organically preserved, spherical to globular, usually with profuse (sometimes laminate) mucilagenous sheath. Daughter colonies often attached. Individual spherules without envelopes, small (0·5 to 2·0 μm), embedded in common mucilage, uniformly distributed throughout colony; spherules spherical, vesicular (hollow), or condensed.

EXPLANATION OF PLATE 1

Figs. 1, 2. *Eosynechococcus thuleënsis*. 1, Holotype, KS78-23a (N15/2), ×2000. 2, end-to-end paired set, KS78-23a, ×2000.

Fig. 3. Spheroid type A., KS78-23e, ×2000.

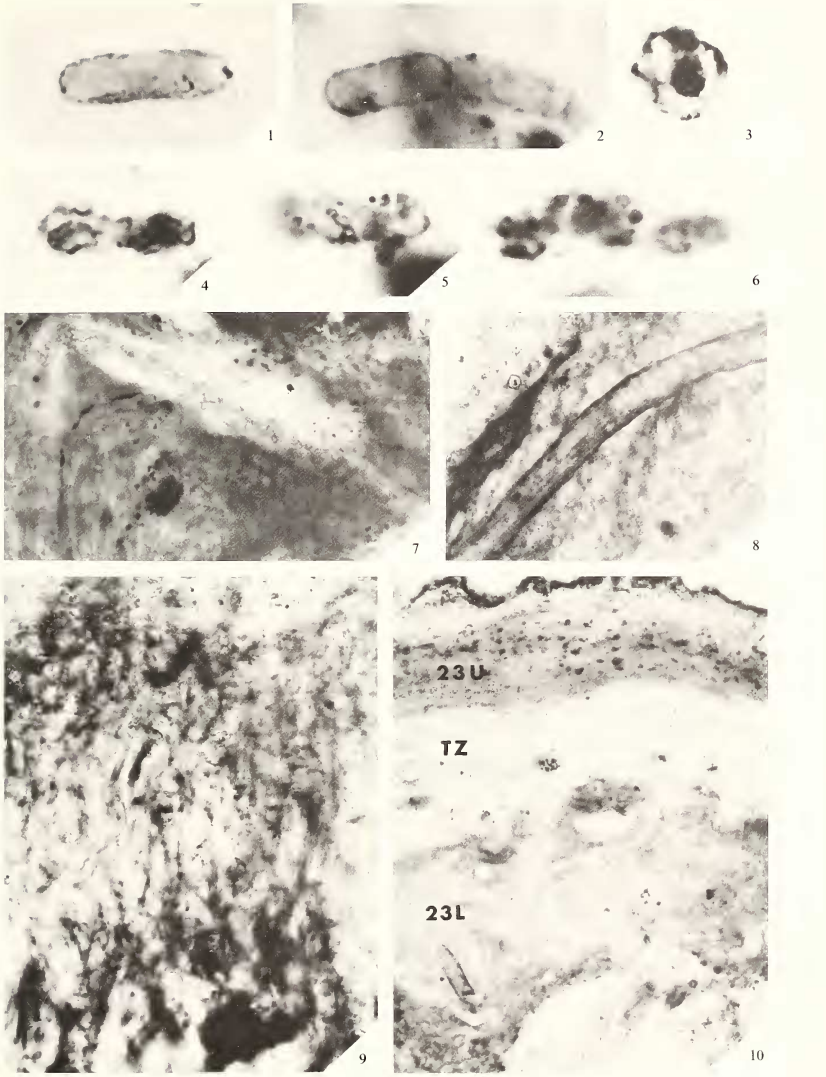
Figs. 4–6. *Eosynechococcus thuleënsis* in stages of degradation KS78-23a, ×2000. 4, paired cells with attached vesicular blebs. 5, degraded unicell. 6, degraded pair in which one cell is reduced to amorphous organic matter.

Fig. 7. Carbonate pseudomorph after *Siphonophycus*, filamentous mat, KS78-23d, ×500.

Fig. 8. *Siphonophycus* cf. *kestron* with interior trichome (non-septate) preserved in sheath lumen, filamentous mat, KS78-23a, ×335.

Fig. 9. *Eomycetopsis robusta* in vertically aligned portion of filamentous mat, KS78-23c, ×1000.

Fig. 10. Thin section of portion of slide KS78-23a showing upper *Eosynechococcus thuleënsis* zone (23U) overlying a silicified carbonate transition layer (TZ), which, in turn, overlies the filamentous (23L) mat. Note large sheaths of *Siphonophycus* cf. *kestron* in lower part, ×150.



STROTHER, KNOLL and BARGHOORN, Late Precambrian micro-organisms

Coleogleba auctifica sp. nov.

Plate 5, figs. 1–3

Diagnosis. As for genus but with colony size ranging from 40 to 170 μm in diameter. Sheath may be characterized by containing tangentially oblate spherules or condensed kerogen.

Holotype. Figured in Pl. 5, fig. 3. Slide No. KS78-18a. England finder co-ordinates, J42/1. HPC No. 60468.

Etymology. From the Latin for 'growing' as indicated by the tendency for daughter colonies to remain attached to parent colonies.

Discussion. Morphologically *C. auctifica* is certainly related to *Microcystis* Kützing, a multicellular chroococcalian cyanophyte found in freshwater plankton blooms. Most species of *Microcystis* are irregularly shaped, but spherical colonies do occur—for example, *M. incerta* and *M. pulvera* (Smith 1933, p. 61). Daughter colony formation in *C. auctifica* is similar to that in *Microcystis*. The sporadic distribution of *C. auctifica* throughout the Aorfêrneq cherts suggests that the organism was planktonic in ephemeral ponds.

Genus EOSYNECHOCOCCUS Hofmann, 1976

Type species. Eosynechococcus moorei Hofmann, 1976, p. 1057, Pl. 2, fig. 4.

Eosynechococcus thuleënsis sp. nov.

Plate 1, figs. 1, 2, 4–6

Diagnosis. Rods 3·0 to 4·6 μm wide, 5 to 25 μm long (mean 3·9 × 10·8 μm); cell contents usually absent, when present, they are homogeneous and never condensed to discrete granules or 'spots', cell surface microgranulate; smaller cells often attached in end-to-end pairs, rarely in chains of four or more cells; rods straight or slightly bent, rarely clustered laterally: sheath absent; cell division transverse; cells often associated with surficial blebs of vesicular to condensed organic matter.

Holotype. Figured in Pl. 1, fig. 1. Slide No. KS78-23a. England finder co-ordinates, N15/2. HPC No. 60470.

Etymology. With reference to the Thule district of north-west Greenland.

Discussion. Morphologically and with respect to cell division, *E. thuleënsis* is remarkably congruent with the extant *Synechococcus* Nägeli. This similarity extends to the tendency for paired cells to remain attached end-to-end after division (*synechos* is Greek for 'holding together'). Unfortunately for the purposes of palaeoenvironmental reconstruction, the physiological tolerances of the extant *Synechococcus* are very wide, so that living species range from marine planktonic (Waterbury *et al.* 1979) to freshwater thermophilic (Brock 1978). *Synechococcus* is not known as a mat-former from marine environments, but Desikachary (1959) reports species from soils and submerged

EXPLANATION OF PLATE 2

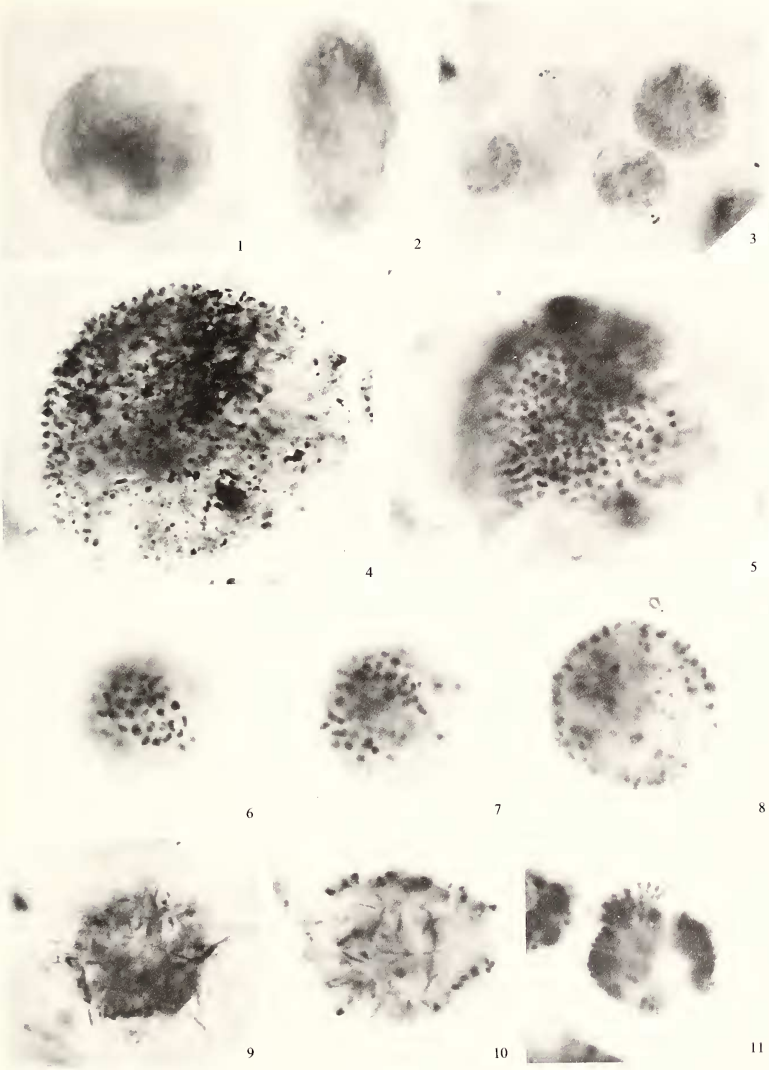
Figs. 1–3. Spheroid type B. 1, typical form, KS78-12h, × 1500. 2, elongate, possibly dividing form, KS78-12i, × 1500. 3, cluster within banded chert, KS78-12h, × 1000.

Figs. 4, 5. *Gyalosphaera fluitans* KS78-12k, × 1000. 4, view in median focus with degraded, unorganized interior contents. 5, surficial view showing spherule arrangement.

Figs. 6–8. *Gyalosphaera fluitans*. Holotype. Three optical planes of the specimen, KS78-12h (H25/3), × 1500.

Figs. 9, 10. *Gyalosphaera fluitans*. 9, degraded specimen with attached filaments, KS78-12h, × 1000. 10, median focus view of degraded specimen with interior rod-shaped structures, KS78-12h, × 1500.

Fig. 11. *Gyalosphaera* cf. *fluitans*. Spherules attached to radially bifurcating stalks are apparent in this median section, KS78-23f, × 1500.



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aquatic habitats and *Synechococcus lividus* is found in hot springs mats in associations with *Chloroflexis* (Doemel and Brock 1974).

E. thuleënsis is distinguished from other species primarily on the basis of size and tendency for its width to remain constant. It is most similar to *E. medius* Hofmann, which is known from only three specimens.

Eosynechococcus amadeus Knoll and Golubic, 1979

Plate 3, fig. 8

1979 *Eosynechococcus amadeus*; Knoll and Golubic, p. 148, fig. 4*c*.

Discussion. The single figured cluster of cells is remarkably similar to the type material from the Bitter Springs Formation. This includes in addition to the size and shape of individual cells, the construction of packets of cells which occur in 'densely packed clusters and curved palisade-like arrangements' (Knoll and Golubic 1979, p. 148).

Eosynechococcus cf. *amadeus* Knoll and Golubic, 1979

Plate 3, fig. 10

Discussion. On the basis of size and shape, cells from clusters that do not mimic exactly the packets formed by *E. amadeus* are considered as *Eosynechococcus* cf. *amadeus*. This type of *Eosynechococcus* is found rarely throughout the *Gyalosphaera* association and parts of the *E. thuleënsis* (23U) association.

Genus MYXOCOCCOIDES Schopf, 1968

Type species. Myxococcoides minor Schopf, 1968, p. 676, pl. 81, fig. 1.

Myxococcoides sp.

Plate 5, fig. 4

1976 Acritarchs (Evitt); Hofmann, p. 1072, pl. 3, figs. 8, 9.

Discussion. Many of the unicells from sample KS78-24 resemble what Hofmann (1976, pl. 3, figs. 8, 9) labelled 'Acritarcha'. In the Aorfêrneq chert, the polygonal outlines of these specimens (Pl. 3, fig. 4) are in all likelihood produced diagenetically as they often contain carbonate crystals in their lumens. *Myxococcoides* Schopf is a form genus encompassing smooth-walled spheroids in the size

EXPLANATION OF PLATE 3

Figs. 1, 2. *Gyalosphaera fluitans*. 1, degraded specimen with attached filaments, KS78-12c, ×1900. 2, large form with dense interior, KS78-12c, ×1000.

Figs. 3–6. *Oscillatoriopsis variabilis*. 3, type specimen exhibiting well-preserved homogeneous contents and straight walls, KS78-12c (K17/2), ×500. 4, specimen with spool-shaped cells including terminal cell, KS78-12D/2, ×500. 5, filament with well-preserved spherical (plasmolysed) protoplasts, KS78-12j, ×1000.

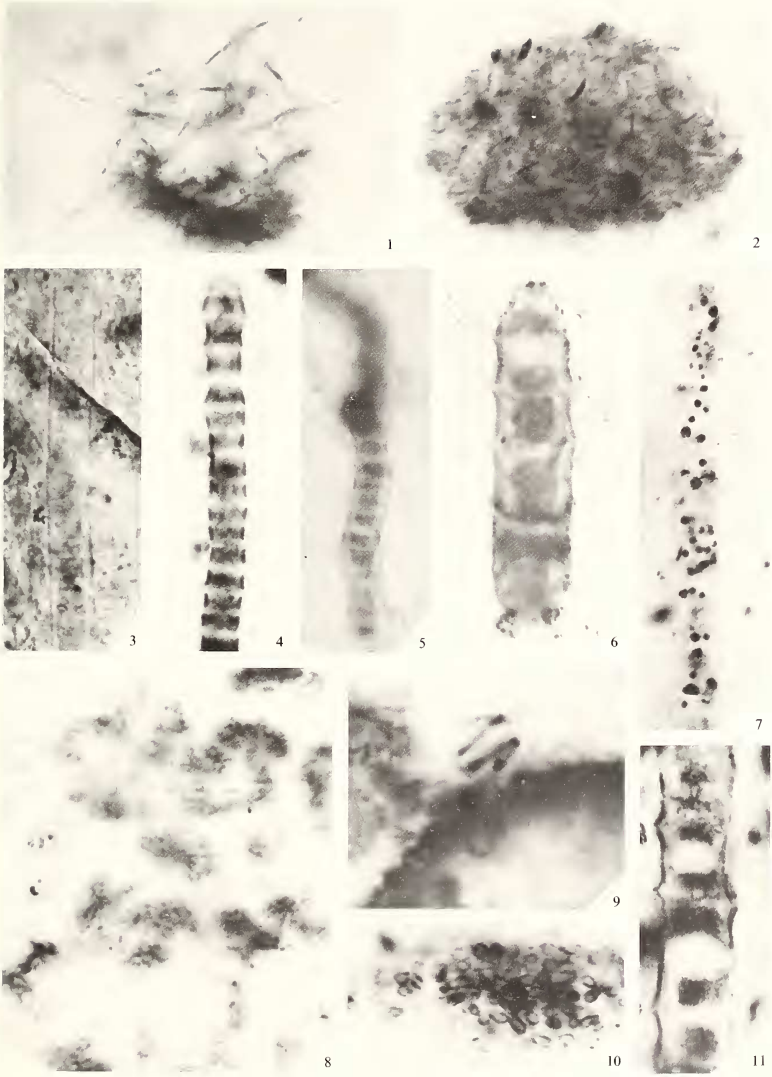
Fig. 7. *Oscillatoriopsis* sp. with dark, granular internal bodies, KS78-12L, ×1000.

Fig. 8. *Eosynechococcus amadeus* showing typical clustering arrangement also in the Bitter Springs samples, KS78-12k, ×1500.

Fig. 9. *Avictuspirulina minuta* type specimen, shown attached to the perimeter of a large *Gyalosphaera*, KS78-12c (G13/4), ×2000.

Fig. 10. *Eosynechococcus* cf. *amadeus* showing a different clustering habit from that in fig. 8, KS78-12i, ×1500.

Fig. 11. *Oscillatoriopsis variabilis* with condensed cell contents and remnant cytoplasm, KS78-12L, ×1000.



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range of 3 to 30 μm. Certainly, the Aorfêrneq spheroids belong to this genus, but preservation is too poor to permit specific designation.

Genus GLOEODINIOPSIS Schopf, 1968

Type species. Gloeodiniopsis lamellosa Schopf, 1968, p. 684, pl. 84, fig. 2.

Gloeodiniopsis cf. *lamellosa* (Schopf) Knoll and Golubic, 1979

Plate 5, figs. 6, 7

Discussion. The Aorfêrneq specimens occur in loosely aggregated clusters of solitary cells that vary from those containing well-laminated sheaths (Pl. 5, fig. 6) to those without thick sheath (Pl. 5, fig. 7). They vary from *G. lamellosa* Knoll and Golubic in their larger size, approaching 20 μm in diameter.

Genus TETRAPHYCUS Oehler, 1978

Type species. Tetraphycus gregalis Oehler, 1978, p. 294, fig. 9J.

Tetraphycus sp.

Plate 5, fig. 5

Discussion. One cluster of cells occurring consistently in planar tetrads and with differentiated cross walls can be placed into the genus *Tetraphycus*, although the distinct wall morphology is unknown from other *Tetraphycus* specimens. Too few cells were found to characterize a new species, the distinguishing characteristics of these cells may have been degradationally induced.

'Chroococcoid unicells'

Chroococcoid unicell type A

Plate 4, fig. 1

Discussion. One population of thirty-two cells contained poorly preserved dyads and tetrads of ensheathed cells. Cells are large, about 30 μm including the thick, conspicuous sheath. The presence of a distinct sheath and the clustering of cells in dyads and tetrads indicates an affinity with *Chroococcus* Nägeli or perhaps *Gloeocapsa* Kützing.

Chroococcoid unicell type B

Plate 4, fig. 2

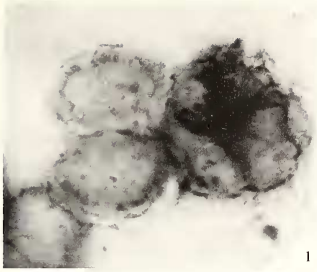
Discussion. A single, large cell with distinct sheath occurred in sample KS78-24. The morphology is decidedly chroococcalean. Elliptical shape and median constriction of the protoplast suggest that this specimen entered into early stages of binary fission shortly before death.

EXPLANATION OF PLATE 4

Fig. 1. 'Chroococcalean unicell' type A, dyad and tetrad with sheath, KS78-12j, ×875.

Fig. 2. 'Chroococcalean unicell' type B, single cell with distinct sheath and constricted median zone, KS78-24g, ×1150.

Figs. 3–8. *Eosynechococcus* cf. *belcherensis*. 3, small clusters of tetrads, KS78-18/f2, ×2000. 4, typical large loosely aggregated cluster, KS78-18/f2, ×500. 5, radially aligned colony, KS78-18A, ×1000. 6, small cluster, KS78-18/f2, ×2000. 7, palisade-forming colony, KS78-18/f2, ×600. 8, loosely associated cells showing variation in size and contents, KS78-18/f2, ×2000.



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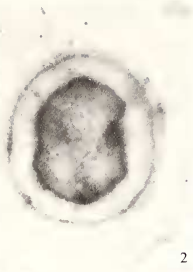

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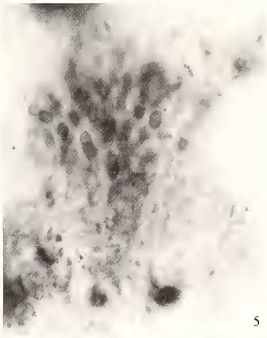

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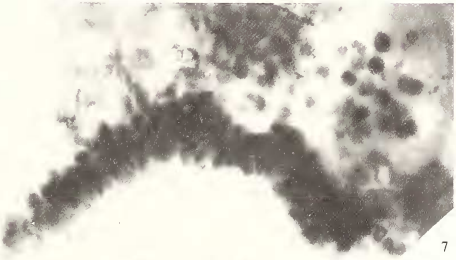

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8

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Family ENTOPHYSALIDACEAE Geitler, 1925
Genus EOENTOPHYSALIS (Hofmann) Mendelson and Schopf, 1982

Type species. Eoentophysalis belcherensis Hofmann, 1976, p. 1070, pl. 6, fig. 13.

Eoentophysalis cf. *belcherensis* Hofmann, 1976

Plate 4, figs. 4–8

Discussion. Numerous colonies of cells dividing in three planes produce a variety of cluster morphologies. These arrangements differ from *E. belcherensis* Hofmann in that forms with internal contents and peripheral colony pigmentation are not apparent in the Greenland material. Their absence may well reflect degradational differences and be of little taxonomic importance. Specimens may be preserved as individual cells embedded in common mucilage or as envelopes of multiple cells in common mucilage. Growth of the clusters is centrifugal, with the result that degraded cores are common in larger aggregates.

Class HORMOGONEAE Thuret, 1875
Order NOSTOCALES Geitler, 1925
Family OSCILLATORIACEAE (S. F. Gray) Dumortier ex Kirchner, 1898
Genus OSCILLATORIOPSIS (Schopf) Mendelson and Schopf, 1982

Type species. Oscillatoriopsis obtusa Schopf, 1968, p. 667, pl. 77, fig. 8.

Discussion. Oscillatoriopsis differs from *Paleolyngbya* Schopf in lacking definite remains of sheath (see Mendelson and Schopf 1982, p. 63).

Oscillatoriopsis variabilis sp. nov.

Plate 3, figs. 3–6, 11

Diagnosis. Organically preserved, fossilized, three-dimensional filaments with cells 14 to 17 μm broad by 7 to 9 μm long; terminal cell hemispherical; cross walls evenly spaced near apices. Cell contents homogeneous, condensed ellipsoidal, condensed spheroidal, or condensed multiple smaller spheroidal bodies; filament margins smooth or crenulate.

Holotype. Figured in Pl. 3, fig. 3. Slide No. KS78-12c. England finder co-ordinates, K17/2. HPC No. 60469.

Etymology. In reference to the variable morphology of cellular contents (which are diagenetically induced) found in this species.

Discussion. O. variabilis is most similar in size to *O. robusta* Horodyski and Donaldson, which is 18 μm wide. *O. robusta* is known from only one specimen in which the cross walls are not organically preserved. *O. variabilis* demonstrates a remarkable sequence of degradational variation (text-fig. 8). The best-preseved specimens are similar to modern *Oscillatoria* in lacking a sheath or having only minimal sheath.

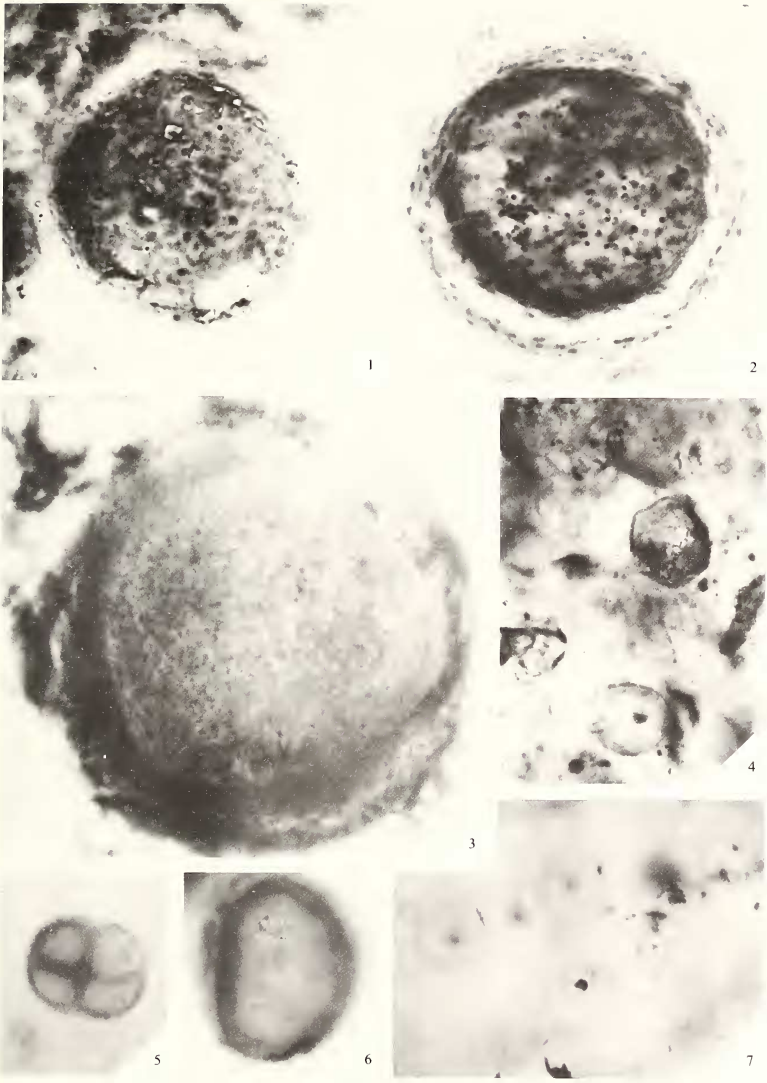
EXPLANATION OF PLATE 5

Figs. 1–3. *Coleogleba auctifica.* 1, small colony with vesicular spherules and minimal sheath, KS78-18/1, × 1000. 2, specimen with condensed spherules and moderate extracolonial mucilage containing flattened spherules, KS78-18/fs, × 1000. 3, type specimen with abundant kerogenous extracolonial mucilage, KS78-18a (J42/1), × 800.

Fig. 4. *Myxococcoides* sp. from thin section KS78-24g, × 1000.

Fig. 5. *Tetraphycus* sp. from KS78-18A showing differentiated wall structure, × 2000.

Figs. 6, 7. *Gloeodiniopsis* cf. *lamellosa.* 6, more typical form with thick laminate sheath, KS78-23c, × 2000. 7, forms with thin sheath and internal protoplasts present, KS78-23a, × 1000.



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Genus AVICTUSPIRULINA gen. nov.

Type species. Avictuspirulina minuta sp. nov.

Diagnosis. Fossilized spiral, cylindrical filament three-dimensionally preserved; more or less regularly coiled; cross walls absent; sheath absent; apices rounded; cell contents uniform and dense; filaments 2 μm or less in diameter.

Etymology. From the Latin *avictus* meaning 'ancestral' and the extant genus *Spirulina* (Turpin) Gardner.

Discussion. Avictuspirulina differs from species of *Heliconema* Schopf in not having a flattened thallus, coils at a 45° angle, and in size and surface texture. It differs from *Obruchevella* Reitl., a Vendian to Ordovician coiled tube, in being less regularly coiled and in size (see Cloud *et al.* 1979).

Avictuspirulina minuta sp. nov.

Plate 3, fig. 9

Diagnosis. As for genus but with filament diameter 0·8 μm wide; filament coiled into three to four spirals 5 to 9 μm in diameter and spaced 2 to 4 μm apart; end spirals often of lesser diameter than middle spirals.

Holotype. Figured in Pl. 3, fig. 9. Slide No. KS78-12c. England finder co-ordinates, G13/4. HPC No. 60466.

Etymology. From the Latin for 'small'.

Discussion. About fifteen specimens of this taxon have been found in association with extracellular organic matter surrounding large *Gyalosphaera*-type organisms. The fossil is morphologically allied to the extant genus *Spirulina* because of its spiral nature and lack of cross walls. *A. minuta* is similar to *Spirulina laxissima* West (Desikachary 1959).

Genus SIPHONOPHYCUS Schopf, 1968

Type species. Siphonophycus kestron Schopf, 1968, p. 671, pl. 80, figs. 1–2.

Siphonophycus sp.

Plate 1, figs. 7, 8, 10

1978 *Siphonophycus* sp. Oehler, p. 300, figs. 12N–12R.

Discussion. Short segments of large (20 to 40 μm) tubes are common in the filamentous (23L) association. Specimens are occasionally infilled with carbonate (Pl. 1, fig. 7) or may contain one or two non-septate trichomes (Pl. 1, fig. 8). Sheath wall is often thick and may consist of a double organic layer. They are comparable to the *Siphonophycus* sp. of Oehler (1978), but preservation is too variable to ascertain useful taxonomic designation.

EXPLANATION OF PLATE 6

Fig. 1. Hand sample, KS78-12, showing carbonate-filled vugs in lower portion and black, fossiliferous chert in upper portion, × 1·4.

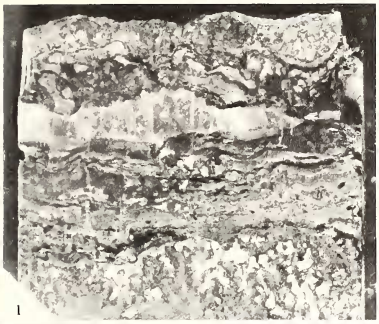
Fig. 2. Thin section, KS78-12j, showing dark, sinuous fossiliferous chert bands, × 3.

Fig. 3. Small pustular stromatolites from locality KS78-18. Sample is partially silicified carbonate, × 1·5.

Fig. 4. Thin section, KS78-18a/5. Gray-laminated portion is unfossiliferous carbonate, dark areas contain abundant *Eoentophysalis* preserved in chert, × 3.

Fig. 5. Thin section, KS78/23f, showing lower vuggy *Eomycetopsis/Siphonophycus* association topped by laminate *Eosynechococcus thuleënsis* zone, × 4.

Fig. 6. Thin section KS78-24 with chert-replaced radiating anhydrite structures, × 4.



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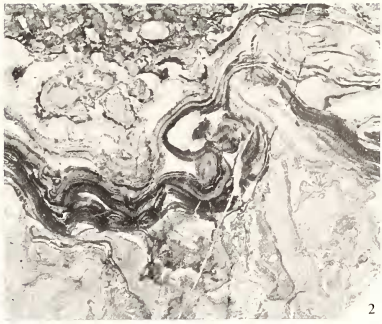

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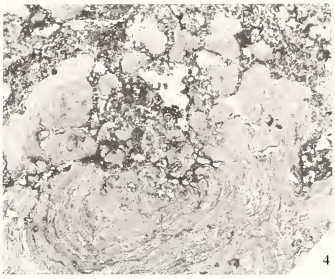

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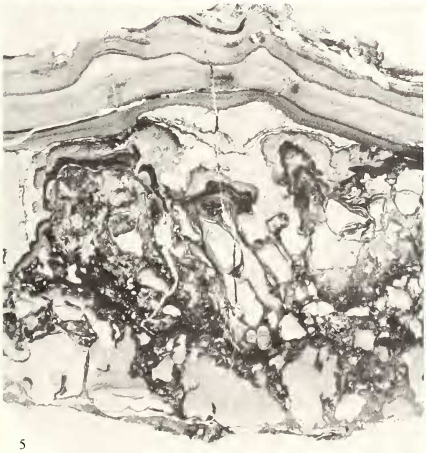

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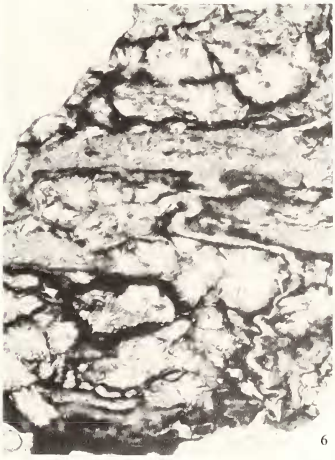

6

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Genus EOMYCETOPSIS (Schopf) Knoll and Golubic 1979

Type species. Eomycetopsis robusta Schopf, 1968, p. 685, pl. 83, fig. 1.

Eomycetopsis robusta Schopf

Plate 1, fig. 9

(for synonomy, see Mendelson and Schopf 1982)

Discussion. Numerous filaments, aseptate and unbranched fit the size characteristics established for this form taxon (2 to 4 μm). The filaments occur in dense, poorly preserved, intertwined mats often with gross vertical alignment. They dominate the filamentous mat (23L) section of sample KS78-23.

Incertae sedis
Spheroid type A

Plate 1, fig. 3

Description. Organically preserved, irregularly shaped, subspherical fossilized envelope often with dense central body; envelope 3 to 12 μm in diameter, inner body up to 5 μm in diameter; granular to microgranular surface texture.

Discussion. Spheroid type A has been found only in the *Eosynechococcus* zone from sample KS78-23. A population of $N = 50$ has the following parameters based on diameter: $\bar{x} = 6{\cdot}8$ μm, range from 3 to 12 μm, $s = 1{\cdot}8$ μm. Spheroid type A codominates the community along with *E. thuleënsis*. The irregularity of its envelope is not characteristic of any known cyanobacteria, nor is it similar to degraded cyanobacterial envelopes. It is possible that spheroid type A represents a non-photosynthetic component of the *Eosynechococcus* community.

Spheroid type B

Plate 2, figs. 1–3

Description. Spherical organism, outline faintly preserved but usually quite spherical; interior contents homogeneous or characterized by lighter spherical blebs embedded in a homogeneous organic matrix; extracellular sheath or mucilage absent; mean diameter 16 μm.

Discussion. Spheroid type B dominates the *Gyalosphaera* assemblage. Its simple morphology and faintly preserved interior structure do not allow its classification even to the kingdom level. The size-frequency characteristics for a population of $N = 113$ (text-fig. 5), show a range of 8 to 28 μm ($\bar{x} = 15{\cdot}7$ μm) in diameter with a leptokurtic distribution reminiscent of algal unicell populations. Spheroid type B probably represents a planktonic organism, but its biological affinities are obscure.

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REFERENCES

BARGHOORN, E. S. and TYLER, S. A. 1965. Microorganisms from the Gunflint Chert. *Science*, **147**, 563–577.

BROCK, T. P. 1978. *Thermophilic microorganisms and life at high temperatures*. New York, 465 pp.

CLOUD, P. E., Jr. 1965. Significance of the Gunflint (Precambrian) microflora. *Science*, **148,** 27–35.

—— AWRAMIK, S. M., MORRISON, K. and HADLEY, D. G. 1979. Earliest Phanerozoic or latest Precambrian fossils from the Arabian Shield. *Precambrian Res.* **10,** 73–94.

DAVIES, W. E., KRINSLEY, D. B. and NICOL, A. H. 1963. Geology of the North Star Bugt Area, northwest Greenland. *Meddelelser om Grønland*, **162,** 47 pp.

DAWES, P. R., REX, D. C. and JEPSEN, H. F. 1976. K/Ar whole rock ages of dolerites from the Thule District, western North Greenland. *In* ESCHER, A. and WATT, W. S. (eds.). *Geology of Greenland.* Copenhagen, pp. 61–66.

DESIKACHARY, T. V. 1959. *Cyanophyta.* New Delhi, 686 pp.

DOEMEL, W. N. and BROCK, T. P. 1974. Bacterial stromatolites: origin of laminations. *Science*, **184,** 1083–1085.

GEITLER, L. 1932. Cyanophyceae. *In* RABENHORST, L. (ed.). *Kryptogamen-Flora von Deutschland, Osterreich und der Schweiz*, **14,** Jena, 1196 pp.

GOLUBIC, S. 1976. Organisms that build stromatolites. *In* WALTER, M. R. (ed.), *Stromatolites.* Amsterdam, pp. 114–140.

—— and HOFMANN, H. J. 1976. Comparison of Holocene and mid-Precambrian entophysalidaceae (Cyanophyta) in stromatolitic algal mats: cell division and degradation. *J. Paleont.* **50,** 1074–1082.

HARDIE, L. A. and GINSBURG, R. N. 1977. Layering: the origin and environmental significance of lamination and thin bedding. *In* HARDIE, L. A. (ed.). *Sedimentation on the Modern carbonate tidal flats of northwest Andros Island. Bahamas.* Baltimore, pp. 50–123.

HOFFMAN, P. 1976. Environmental diversity of middle Precambrian stromatolites. *In* WALTER, M. R. (ed.). *Stromatolites.* Amsterdam, pp. 599–611.

HOFMANN, H. J. 1976. Precambrian microflora, Belcher Islands, Canada: significance and systematics. *J. Paleont.* **50,** 1040–1073.

HORODYSKI, R. J. and DONALDSON, J. A. 1980. Microfossils from the Middle Proterozoic Dismal Lake Group, arctic Canada. *Precambrian Res.* **11,** 125–159.

HUMM, H. J. and WICKS, S. R. 1980. *Introduction and guide to the marine blue-green algae.* New York, 194 pp.

KENDALL, A. C. 1979. Continental and supratidal (sabkha) evaporites. *In* WALTER, R. G. (ed.). *Facies models.* Toronto, pp. 145–158.

—— and SKIPWITH, P. A. 1968. Recent algal mats of a Persian Gulf lagoon. *J. Sedim. Petrol.* **38,** 1040–1058.

KNOLL, A. H. 1981. Paleoecology of late Precambrian microbial assemblages. *In* NIKLAS, K. J. (ed.). *Paleobotany, Paleoecology, and Evolution.* New York, pp. 17–54.

—— 1982*a*. Microorganisms from the late Precambrian Draken Conglomerate, Ny Friesland, Spitsbergen, *J. Paleont.* **56,** 755–790.

—— 1982*b*. Microbiotas of the late Precambrian Hunnberg Formation, Nordaustlandet, Svalbard. Ibid., in press.

—— BARGHOORN, E. S. and AWRAMIK, S. M. 1978. New microorganisms from the Aphebian Gunflint Iron Formation, Ontario. Ibid. **52,** 976–992.

—— and GOLUBIC, S. 1979. Anatomy and taphonomy of a Precambrian algal stromatolite. *Precambrian Res.* **10,** 115–151.

—— and SIMONSON, B. 1981. Early Proterozoic microfossils and penecontemporaneous quartz cementation in the Sokoman Iron Formation, Canada. *Science*, **211,** 478–480.

—— and VIDAL, G. 1980. Late Proterozoic vase-shaped microfossils from the Visingso Beds, Sweden. *Geol. Foren. Stockholm Forh.* **102,** 207–211.

KRUMBEIN, W. E., BUCHHOLZ, H., FRANKE, P., GIANI, D., GIELE, C. and WONNEBERGER, K. 1979. Oxygen and hydrogen sulfide coexistence in stromatolites: a model for the origin of mineralogical lamination in stromatolites and banded iron formations. *Naturwissenschaften*, **66,** 381–389.

KURTZ, V. E. and WALES, D. M. 1959. Geology of the Thule Area, Greenland. *Proc. Okla. Acad. Sci.* 1950, 83–89.

LICARI, G. R., CLOUD, P. E. and SMITH, W. D. 1969. A new chroococcaceaen alga from the Proterozoic of Queensland. *Proc. natn. Acad.* **62,** 56–62.

LOGAN, B. W., REZAK, R. and GINSBURG, R. N. 1964. Classification and environmental significance of algal stromatolites. *J. Geol.* **72,** 68–83.

MARGULIS, L., ASHENDORF, D., BANERJEE, S., FRANCIS, S., GIOVANNOI, S., STOLZ, J., BARGHOORN, E. S. and CHASE, D. 1980. The microbial community in the layered sediments at Laguna Figueroa, Baja California. *Precambrian Res.* **11,** 93–124.

MENDELSON, C. V. and SCHOPF, J. W. 1982. Proterozoic microfossils from the Sukhaya Tunguska, Shorikha, and Yudoma Formations of the Siberian Platform, USSR. *J. Paleont.* **56,** 42–83.

MONTY, C. 1976. The origin and development of cryptalgal fabrics. *In* WALTER, M. R. (ed.). *Stromatolites*. Amsterdam, pp. 193–249.

MUIR, M. D. 1976. Proterozoic microfossils from the Amelia Dolomite, McArthur Basin, Northern Territory. *Alcheringa*, **1**, 143–158.

OEHLER, D. Z. 1978. Microflora of the middle Proterozoic Balbarini Dolomite (McArthur Group) of Australia. Ibid. **2**, 269–309.

——OEHLER, J. H. and STEWART, A. 1979. Algal fossils from a late Precambrian hypersaline lagoon. *Science*, **205**, 388–390.

OEHLER, J. H. 1977. Microflora of the H.Y.C. Pyritic Shale Member of the Barney Creek Formation (McArthur Group), middle Proterozoic of northern Australia. *Alcheringa*, **1**, 315–349.

PARK, R. K. 1977. The preservation potential of recent stromatolites. *Sedimentology*, **24**, 485–506.

PEAT, C. J., MUIR, M. D., PLUMB, K. A., MCKIRDY, D. M. and NORVICK, M. S. 1978. Proterozoic microfossils from the Roger Group, Northern Territory, Australia. *BMR J. Australian Geol. Geophys.* **3**, 1–17.

PURSER, B. H. 1973. *The Persian Gulf: Holocene carbonate sedimentation and diagenesis in a shallow epicontinental sea*. Berlin, 471 pp.

SCHOPF, J. W. 1968. Microflora of the Bitter Springs Formation, late Precambrian, central Australia. *J. Paleont.* **42**, 651–688.

——1977. Earliest evidence of fossil eukaryotes. *In* PONNAMPERUMA, C. (ed.). *Chemical evolution of the Early Precambrian*. New York, pp. 107–109.

SHEARMAN, D. J. 1978. Evaporites of coastal sabkhas. *In* DEAN, W. E. and SCHREIBER, B. C. (eds.). *Marine evaporites*. SEPM Short Course No. 4, pp. 6–42.

SMITH, G. M. 1933. *The fresh-water algae of the United States*. New York, 716 pp.

STROTHER, P. K. 1980. *Microbial communities from Precambrian strata*. Thesis, Harvard University.

VIDAL, G. 1981. Micropalaeontology and biostratigraphy of the Upper Proterozoic and Lower Cambrian sequence in East Finnmark, northern Norway. *Norges geol. Unders.* **362**, 1–53.

——and DAWES, P. R. 1980. Acritarchs from the Proterozoic Thule Group, north-west Greenland. *Grønlands geol. Unders. Rap.* **100**, 24–29.

——and KNOLL, A. H. (in press). Proterozoic plankton. *Geol. Soc. Amer. Mem.*

WALTER, M. R., GOODE, A. D. T. and HALL, W. D. M. 1976. Microfossils from a newly discovered Precambrian stromatolitic iron formation in western Australia. *Nature*, **261**, 221–223.

WATERBURY, J. B., WATSON, S. W., GUILLARD, R. R. L. and BRAND, L. E. 1979. Widespread occurrence of a unicelular, marine, planktonic cyanobacterium. Ibid., **277**, 293–294.

WOOD, G. V. and WOLFE, M. J. 1969. Sabkha cycles in the Arab/Darb Formation of the Trucial Coast of Arabia. *Sedimentology*, **12**, 165–191.

ZHANG, Z. 1981. Precambrian microfossils from the Simian of South China. *Nature*, **289**, 792–793.

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